

***Streblospio gynobranchiata*, a new spionid polychaete species  
(Annelida: Polychaeta) from Florida and the Gulf of Mexico with an  
analysis of phylogenetic relationships within the genus *Streblospio***

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*Abstract.*—*Streblospio gynobranchiata*, a new species of spionid polychaete, is described from Florida and the Gulf of Mexico. This species is distinguished by the presence of strap-like branchiae, beneath which larvae are brooded, in the genital body region of the females. Data from experimental crosses conducted in the laboratory are presented that indicate incipient reproductive isolation between *S. gynobranchiata* from Florida and *S. benedicti* from North Carolina and California. The spermatophores produced by males of *S. gynobranchiata* and *S. benedicti* are described for the first time. Morphological, developmental, and reproductive characteristics are used in combination to construct a cladogram that suggests possible phylogenetic relationships between known species in the genus *Streblospio*.

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Genus *Streblospio* Webster, 1879

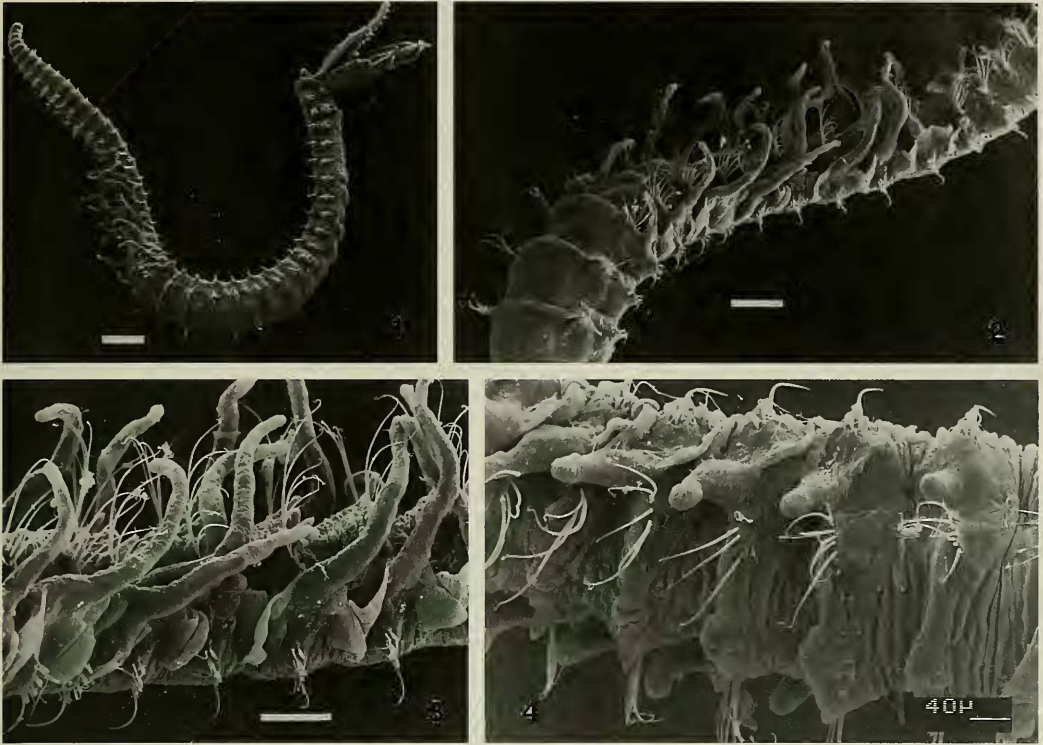
*Diagnosis.*—The genus *Streblospio* was established by Webster (1879) based upon material from New Jersey. Distinguishing features of the genus include: conical, rounded prostomium with 2-4 pairs of eyes and with or without a small nuchal tentacle; peristomium fused with the first setiger and forming a U-shaped envelope around the prostomium laterally and ventrally; one pair of palps and one pair of branchiae on the peristomium; a dorsal collar across the dorsum of setiger 2; notosetae all capillary, neurosetae include capillaries, multidentate hooded hooks and ventral sabre setae; and pygidium simple, with ventral lappets or without appendages.

*Streblospio gynobranchiata*, new species  
Figs. 1-13

*Type material.*—Holotype: adult female (USNM 178822), length 8.4 mm, Tampa Bay, Florida; Courtney Campbell Causeway (west): depth 1 m, muddy sand, 27 Jul

1989. Paratypes: 17 males (USNM 178824), 8 females (USNM 178823), same collection data as holotype.

Additional material prepared for scanning electron microscopy (SEM): Stub #1 (USNM 178825)—4 anterior ends, collected 22 Jun 1987, Hillsborough River, Tampa, Florida, at the University of Tampa, depth 2 m, muddy sand; Stub #2 (USNM 178826)—2 adults, collected 23 Mar 1987, same as Stub #1; Stub #3 (USNM 178827)—4 anterior ends, collected 4 Aug 1988, same coll. data as holotype; Stub #5 (USNM 178828)—4 anterior ends, same coll. data as Stub #3; Stub #7 (USNM 178829)—4 adults, coll. 26 Mar 1987, same coll. data as holotype; Stub #8 (USNM 178830)—5 adult females, coll. 2 May 1987, same coll. data as holotype; Stub #9 (USNM 178831)—5 adults, same coll. data as Stub #8; Stub #10 (USNM 178832)—6 adults, same coll. data as Stub #8; Stub #11 (USNM 178833)—3 adults, coll. 1 Apr 1987, same coll. data as holotype.



Figs. 1–4. *Streblospio gynobranchiata*, new species (USNM 178830): 1, whole female with characteristic brood structures; 2, posterior dorsal portion of female showing strap-like brood structures; 3, lateral view of brood structures in female; 4, dorsal view of most anterior brood structures and notosetae. Scales = 200  $\mu$ m for 1; 100  $\mu$ m for 2, 3.

*Other material examined.*—Massachusetts: Provincetown, coll. H. E. Webster, type (USNM 415), 6 specimens + 3 fragments; San Francisco Bay, Berkeley Beach, coll. O. Hartman, 27 Jul 1934, (USNM 20220) 8 paratypes; New Jersey, Little Egg Inlet, coll. 17 Apr 1972, (USNM 71677) 8 specimens, (USNM 71678) 22 specimens; SEM preparations: Box #7, Stub #4—1 anterior end, Stub #6—3 anterior ends, coll. Bogue Sound, North Carolina, coll. L. Levin; Cultured material: Sebastian River, Florida, 29 Mar 1993; Copano Bay, Texas, 18 Oct 1983; Godineaux, Trinidad 3 Apr 1984; Ballast Point, Tampa Bay, Florida 6 Jun 1984.

*Distribution.*—*Streblospio gynobranchiata* has been collected from the east and west coasts of Florida, Texas, and Trinidad. The type locality is Tampa Bay, Florida in

the subtidal estuarine sediments of the Hillsborough River adjacent to the University of Tampa in downtown Tampa.

*Etymology.*—The specific name, *gynobranchiata*, refers to the branchiate brood structures found in mature females of this species. The prefix is from the Greek, *gyne*, meaning woman or female plus the suffix from the Greek, *branchia*, referring to “gills.”

*Description.*—Prostomium elongate and rounded anteriorly, flanked laterally by peristomial ridges leading to ventral mouth. One pair of palps located lateral to prostomium and median to peristomial ridges. Palps short; about same length as adjacent branchiae and densely ciliated on frontal surfaces (Figs. 1, 5). One pair of thick, ciliated branchiae inserted just posterior to palps. These branchiae with dis-

tal digitiform appendage terminally (Fig. 6). Small conical nuchal tentacle present between branchiae (Fig. 7). Nuchal tentacle difficult to see without removing branchiae.

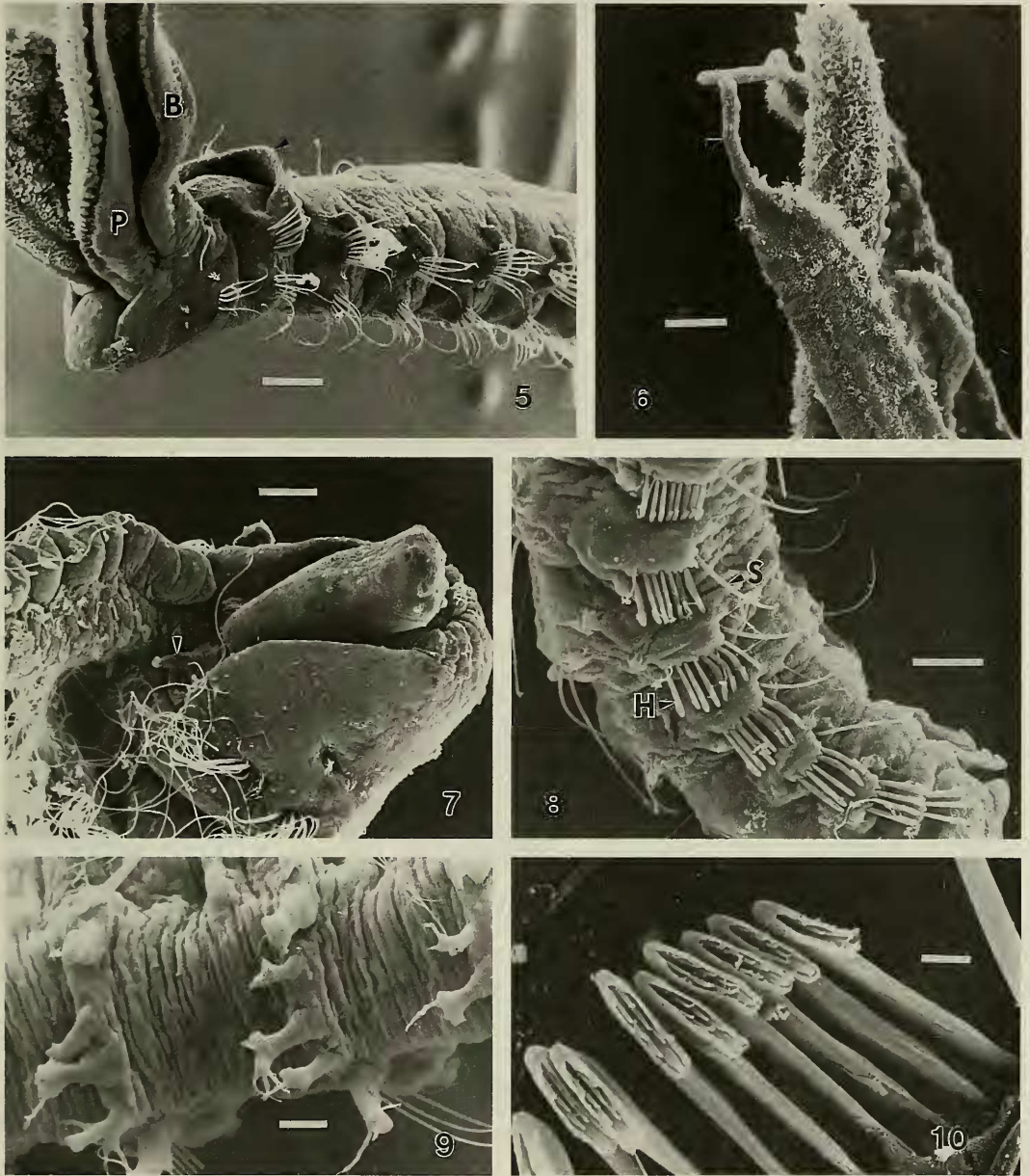
Notopodium of setiger 1 with 1–3 capillary setae and no postsetal lobe (Fig. 5). First neuropodium with 3–6 capillary setae and flap-like postsetal lobe. Second notopodium with 6–12 capillary setae and broad, postsetal lobe continuous with dorsal hood that extends across dorsum connecting left and right notopodia. Anterior margin of hood flares upward and forms opening into dorsal pouch that extends posteriorly to end of third setiger (Fig. 5). Second neuropodium with 6–8 capillary setae and broad flap-like postsetal lobe. Notopodia of females situated along lateral sides of body anterior to branchiate region but shifted dorsally throughout branchiate region (setigers 20–35) and on posterior setigers. Notosetae in branchiate and posterior body regions longer than anterior notosetae. Notopodial lobes flap-like through anterior one-half of body, becoming digitiform and shifted dorsally toward posterior. Neurosetae capillary in setigers 1–6. Ventralmost capillary seta in neuropodia 3–6 stouter than others and curving ventrally under body. Neuropodial hooded hooks and sabre setae beginning on setiger 7 and continuing to end of body (Figs. 8, 10). Hooded hooks accompanied by 1–3 small anterior capillary setae to near end of body. Single inferior sabre seta present in each neuropodium from setiger 7 to end of body (Fig. 8). Hooded hooks number 2–4 in setiger 7 to 6–8 near end of body; each hook with three or four pairs of small teeth in addition to main unpaired tooth (Fig. 10). Neuropodial lobes flap-like on setigers 1–6, decreasing in size posteriorly.

Brood structures present on females from about setiger 20 to about 35 (24–35 in holotype), small in anterior and posterior regions, reaching maximum size in middle of range (Figs. 1–4). Largest pouches composed of broad semicircular fold arising lat-

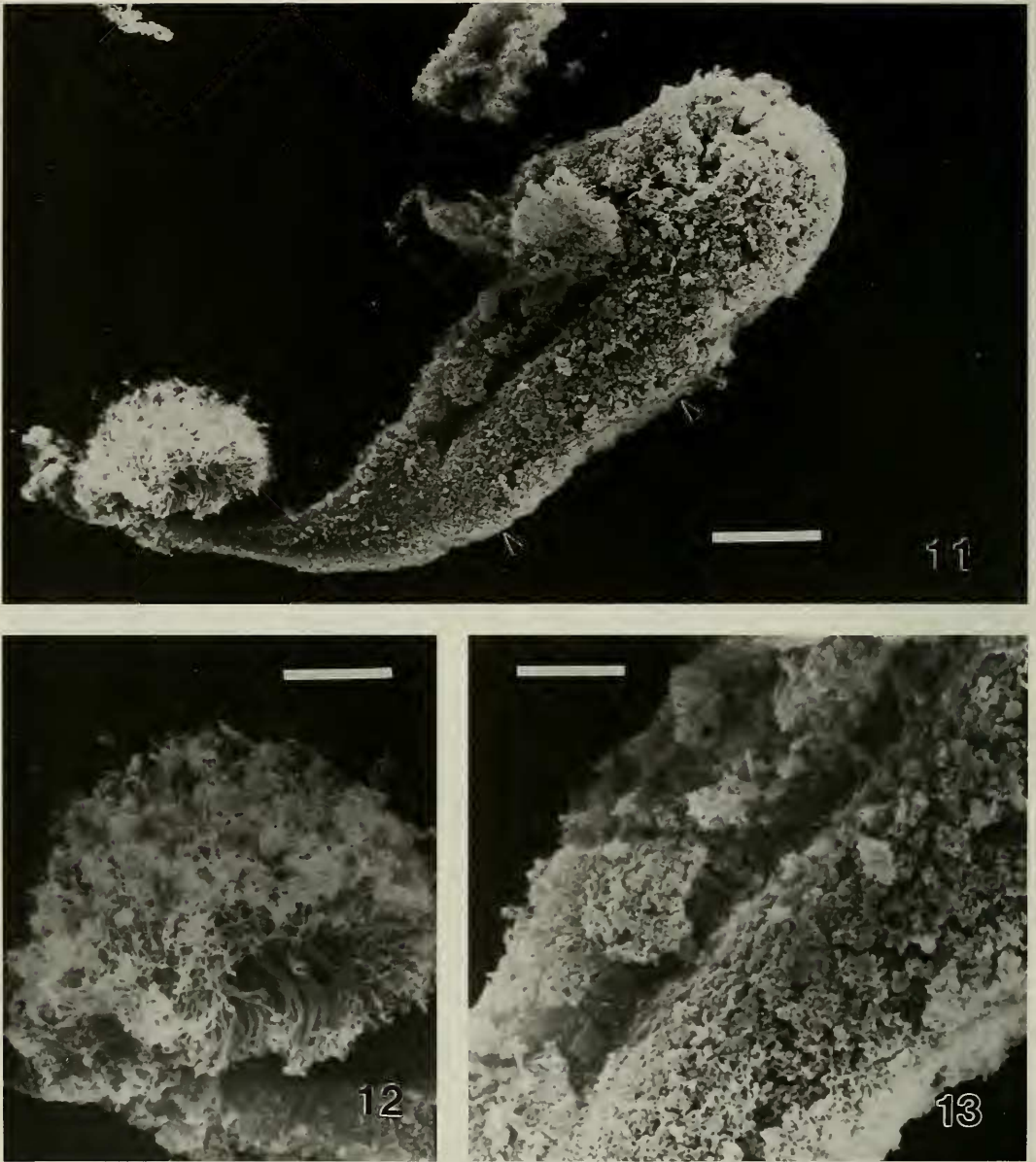
erally between noto- and neuropodium and extending dorsally as thin digitiform appendage resembling a branchium. Developing larvae loosely held between branchiae by brooding females. Posterior to branchiate region on females are dorsal, segmentally arranged extensions of epidermis forming branched, ciliated appendages in rows between left and right notopodia (Fig. 9). Three or four of these extensions present on posterior setigers to near end of body. Cilia on these epidermal extensions arranged in discrete tufts.

Males of *Streblospio gynobranchiata* produce spermatophores in laboratory cultures in the presence or absence of females. These spermatophores are composed of a sickle-shaped proximal piece and a distal sperm ball (Fig. 11). The proximal piece is divided into two regions: a thick coarsely granular region (0.28 mm long and 0.12 mm wide) further from the sperm ball and a curved, conical, tapering region (0.24 mm long and 0.08 mm wide at widest point) leading to and attached to the sperm ball. The former, thick region has a groove down one side that ends at the junction between it and the conical region (Figs. 11, 13). The conical region is smoother than the thick region. The sperm ball measures 0.51 mm in diameter and is spherical in shape (Fig. 12). The dimensions of the spermatophore components vary with the size of the worm producing them, with larger worms releasing larger spermatophores. In cross-section, the material making up the thick and conical regions of the spermatophore appears to be composed of fibrous material of unknown composition. The sperm ball is surrounded by a thin layer of this fibrous material. Only mature sperm are found inside the sperm ball. These sperm are oriented parallel to each other and closely packed inside the sperm ball with their tails extending in a single direction. In fresh spermatophores, the sperm tails have a refringent color in reflected light and move in slow synchronous beating motions. Spermatophores of the same general structure as





Figs. 5–10. *Streblospio gynobranchiata*, new species (5, 9, USNM 178829; 6, USNM 178831; 7, USNM 178828; 8, 10, USNM 178830): 5, lateral view of anterior end with branchia (B), palp (P), and hood (arrow) visible; 6, distal tip of branchium showing finger-like extension (arrow); 7, lateral view of anterior end with right palp and branchium removed to expose the nuchal antenna (arrow); 8, lateral view of posterior setigers showing hooded hooks (H) and sabre setae (S), sabre setae are ventral to the hooded hooks; 9, dorsal view of female posterior to brood structures showing segmental epidermal extensions with tufts of cilia; 10, hooded hooks from posterior setiger showing pairs of small teeth distal to the main tooth. Scales = 100  $\mu\text{m}$  for 5; 50  $\mu\text{m}$  for 6, 7; 25  $\mu\text{m}$  for 8, 9; 5  $\mu\text{m}$  for 10.



Figs. 11–13. *Streblospio gynobranchiata*, new species: 11, whole spermatophore as released by male; arrows indicate region enlarged in Fig. 13; 12, sperm ball attached to end of spermatophore; 13, central portion of spermatophore (region between arrows in Fig. 11) showing central groove and texture of material of spermatophore. Scales = 100  $\mu\text{m}$  for 11; 25  $\mu\text{m}$  for 12, 13.

described above were produced in laboratory cultures of *S. benedicti* from North Carolina and Los Angeles. The mature sperm of *S. gynobranchiata* are greatly elongate with a mean head length (nucleus plus acrosome) of 41.15  $\mu\text{m}$  ( $n = 150$ ).

*Biology.*—*Streblospio gynobranchiata* is found in estuarine to marine conditions in shallow-water sediment. Worms may form dense assemblages of tubes in stressed or disturbed habitats. Larval development is planktotrophic with brood-



ing to the three-setiger stage followed by release into the plankton and settlement at about 9–12 setigers. Females that are forced to leave their tubes while brooding may drop their embryos prematurely. Male worms produce spermatophores (described above) that are incorporated into ventrally located seminal receptacles in the females. Site of fertilization and transport of mature oocytes into brood structures have not been observed.

*Remarks.*—In Webster's (1879) original description of *Streblospio benedicti*, reference is made to the genital pouches in females: "On one specimen the middle third of the dorsum was covered by a very thin, transparent, raised membrane." (Webster 1879: 121). Webster (1879) did not use the term "pouches" to describe these female structures; however, examination of worms from Little Egg Inlet, New Jersey (USNM 71678) revealed brood pouches on females similar to those typically seen in worms from North Carolina and California. Webster (1879) did not mention what have been called "sabre setae" in the neuropodium from setiger 7 to the end of the body nor did he describe the pairs of small teeth located above the main tooth on neuropodial hooded hooks. He refers to the hooded hook morphology as: ". . . they have four terminal teeth, the outer one being shortest . . ." (Webster 1879: 121). Examination of the material from New Jersey (USNM 71678) by SEM revealed that sabre setae begin in setiger 7 and continue to near the end of the body and that the neuropodial hooded hooks have 3 or 4 pairs of small teeth in addition to the main unpaired tooth. The morphological and reproductive characteristics of the species in the genus *Streblospio* are summarized in Table 1.

Levin (1984) reported that *Streblospio benedicti* displayed different patterns of larval development over its range with some populations producing lecithotrophic larvae and others producing planktotrophic larvae. Planktotrophic and lecithotrophic popula-

tions were shown to be interfertile but females from interpopulational crosses tended to produce larvae characteristic of their original population. The production of different larval types was not affected by temperature or food availability in populations of *S. benedicti* from North Carolina (Levin & Creed 1986), although *S. benedicti* from Narragansett Bay increased brood sizes in response to elevated nutrient levels in mesocosm studies (Levin 1986). The demographic consequences of planktotrophy versus lecithotrophy in *S. benedicti* have been addressed by Levin, et al. (1987), Levin & Huggett (1990) and Levin & Bridges (1994). A genetic basis for this polymorphism in *S. benedicti* was demonstrated by Levin et al. (1991).

Buchanan (1890) described a species, *Streblospio shrubsolii* (originally *Hekaterobranthus shrubsolii*) from Sheppey, England, that differed from *S. benedicti* by lacking a median nuchal tentacle (conical papilla or cirrus) on the first segment, lacking the conical dorsal cirri on posterior setigers, and lacking thoracic nephridia. Additional features of *S. shrubsolii* that distinguish it from *S. benedicti* include: the first appearance of hooded hooks on setiger 8; the apparent lack of ventral sabre setae; the two-lobed dorsal hood on setiger 2; and the 2 rows of small teeth on hooded hooks. Subsequent examinations of this species revealed differences in egg diameter, location of the first gametogenic setiger, larval development, brood structures on females, and isozyme frequencies. According to Cazaux (1985) and our unpublished observations (LAL), *S. shrubsolii* from France exhibit mature ova 200–230  $\mu\text{m}$  in diameter, with one large larva brooded between transverse ridges on each segment. Development is direct in this species. In an examination of four enzyme systems (PHI, MDG-2, ADH, and IDH), individuals of *Streblospio shrubsolii* ( $n = 12$ ) were fixed for completely different isozymes than planktotrophic individuals ( $n = 8-70$ ) and leci-

Table 1.—Morphological and reproductive characteristics of described species of *Streblospio*.

Character	<i>Streblospio gynobranchiata</i> new species	<i>Streblospio benedicti</i> Webster 1879	<i>Streblospio shrubsolii</i> Buchanan 1890	<i>Streblospio japonica</i> Imajima 1990
Body length (mm)	8.4	6–12	6–10	7
No. of segments	70	70	48	48
Pairs of eyes	2–3	2–3	2–4	2
Nuchal antenna on 1st segment	present	present	absent	present
Branchial pairs	1	1	1	1
Start of hooded hooks (setiger)	7	6/7/8/9	8	7
No. hooks per ramus				
anterior	3–4	3–5	2–3	5–6
posterior	8–10	8–12	5	?
Dorsal collar	one piece	one piece	2 lobes	one piece
Brood structures	branchiate	pouches	transverse, mid-segmental ridges	?
First saber seta	7	7	?	3
Rows of small teeth on hooded hooks	3–4	3–4	2	5 pairs
Pygidium	simple	simple or lobed	simple	2 lappets
Egg diameter ( $\mu\text{m}$ )	70–90	70–90 (planktotrophic) 100–220 (lecithotrophic)	200–230	?
Larval development	planktotrophic	planktotrophic and lecithotrophic	Direct	?
Larval swimming setae	yes	yes (planktotrophic) no (lecithotrophic)	no	?
Number of larvae per brood	100–200	200–400 (planktotrophic) 30–70 (lecithotrophic)	?	?
Sperm head length ( $\mu\text{m}$ )	41.15	47.81	?	?

thotrophic individuals ( $n = 10\text{--}60$ ) of *S. benedicti*.

Studies of oogenesis in *Streblospio* have revealed differences in yolk bodies that appear to vary with species and developmental mode. The size of yolk granules and relative proportion of heterosynthetically-derived yolk differs between planktotrophic and lecithotrophic forms of *S. benedicti* (Eckelbarger 1980, 1986). Preliminary ultrastructural studies suggest that average yolk body diameter in *S. shrubsolii* (6.8  $\mu\text{m}$ ) is greater than that in *S. gynobranchiata* (3.2  $\mu\text{m}$ ) from Fort Pierce, or from planktotrophic (2.6–3.2  $\mu\text{m}$ ) or lecithotrophic (3.2–5.3  $\mu\text{m}$ ) *S. benedicti*. The mature egg of *S. shrubsolii* contains large quantities of lipid droplets not evident in

the other species, as well as a different morphology of the egg envelope (K. Eckelbarger, pers. comm.). These differences suggest interspecific divergence in female gamete morphology similar to that reported for sibling species of *Capitella* (Eckelbarger & Grassle 1983).

Horst (1909) described an additional species of *Streblospio* (*S. dekhuyzeni*) from Zuide Zee, France that had two types of capillary notosetae and more hooded hooks per ramus than *S. shrubsolii*. These differences were minor enough to lead most taxonomists to consider *S. dekhuyzeni* and *S. shrubsolii* synonyms (Fonseca-Genevois & Cazaux 1987).

Hartman (1936) described *Streblospio lutincola* from several locations along the

central California coast. She (pg. 46) considered this new species to differ from *S. benedicti* in having a "... much smaller ventral peristomial fold, and its much larger prostomium." *Streblospio lutincola* was later synonymized with *S. benedicti* (Hartman 1944).

Foster (1971) proposed a synonymy of all previously described species making the genus *Streblospio* monotypic. In a note at the end of her treatment of the genus (pg. 115), she mentions a population of *Streblospio* collected from Maracaibo estuary that has branchiate brood structures in females. This appears to be the first mention of *S. gynobranchiata* in the literature.

While *Streblospio gynobranchiata* generally possesses a more southerly distribution than the other described species of *Streblospio*, it has been reported in the same geographical regions as *S. benedicti*. For example, lecithotrophic *S. benedicti* have been collected from Big Slough in Aransas Bay, Texas and *S. gynobranchiata* from an attached estuarine system, Copano Bay, Texas. Planktotrophic *S. benedicti* from Fort Pierce, Florida were collected within a few km of the Sebastian River system where *S. gynobranchiata* occurs. It is unknown whether these patterns of distribution are natural or the result of anthropogenic transport since *Streblospio* may be transported in ship ballast water from one location to another (Carlton 1975).

Imajima (1990) described a new subspecies (*Streblospio benedicti japonica*) from the Yatsu tidelands, Japan. This new form differs from *S. benedicti* in having ventral sabre setae beginning on setiger 3 and by having 5 pairs of small teeth in addition to the main unpaired tooth on the hooded hooks.

The mean length of the sperm (acrosome + nucleus + middlepiece) from spermatophores is significantly different ( $P < 0.001$ ) between *Streblospio gynobranchiata* ( $41.15 \mu\text{m} \pm 4.22$ ,  $n = 150$ ) from Tampa Bay and *S. benedicti* ( $47.81 \mu\text{m} \pm 2.83$ ,  $n = 150$ )

from Los Angeles. The location of the first gametogenic setiger in males of *S. gynobranchiata* ( $15.66 \pm 9.98$ ,  $n = 35$ ) is not significantly different from that of planktotrophs of *S. benedicti* from Fort Pierce ( $9.0 \pm 2.28$ ,  $n = 6$ ).

In females of *Streblospio gynobranchiata*, the location of the first gametogenic setiger is significantly different from that of *S. benedicti* (planktotrophs and lecithotrophs), and *S. shrubsolii* (Table 2). In addition, the percent gametogenic setigers, the location of the first brood structure, and the total number of brood structures is significantly different between *S. gynobranchiata* and *S. benedicti* (Table 2).

Reproductive isolation has been reported between *Streblospio gynobranchiata* from Tampa Bay, Florida and *S. benedicti* from North Carolina and from Los Angeles, California (Rice 1991). Experimental crosses between populations were undertaken with worms that had been raised in isolation until sexual maturity then paired with a mate from an exotic population (experimental) or from the same population (control) and monitored for production of larvae. Females from unsuccessful interpopulational crosses were subsequently paired with males from their own population to ensure female fertility. In 28 reciprocal crosses between Tampa Bay and North Carolina worms, 26 crosses produced no offspring (see Rice 1991, table 11). In six crosses between Tampa Bay females and Los Angeles males, no offspring were produced.

In a separate series of experimental crosses, we were able to successfully cross *Streblospio gynobranchiata* from Copano Bay, Texas with lecithotrophic *S. benedicti* from Big Slough, Texas. We also found larval production in limited crosses between females of *S. gynobranchiata* from Tampa Bay and males (planktotrophic) of *S. benedicti* from Tar Landing, North Carolina, indicating that reproductive isolation between these two (or more) species is not complete.

In an experimental cross between one



Table 2.—Reproductive characteristics of mature females of *Streblospio* species. Underlined mean values are not significantly different ( $P > 0.05$ ).

Characteristic	<i>S. benedicti</i> (planktotrophs)	<i>S. benedicti</i> (lecithotrophs)	<i>S. gynobranchiata</i>	<i>S. shrubsolii</i>	Analysis of Variance
Total setigers					
mean	<u>47.8</u>	<u>45.0</u>	<u>46.6</u>	<u>51.3</u>	F = 1.502
std. dev.	6.4	10.7	11.8	6.5	P = 0.2146
number	68	97	79	6	
First gametogenic setiger					
mean	10.5	12.7	7.7	19	F = 217.2
std. dev.	1.1	1.3	2.0	1.1	P = 0.0001
number	71	80	78	6	
% gametogenic setigers					
mean	<u>38.3</u>	<u>34.6</u>	45.4	—	F = 12.7
std. dev.	8.7	6.8	8.7	—	P = 0.0001
number	6	18	61	—	
First pouch/branchium					
mean	<u>21.2</u>	<u>21.6</u>	20.0	—	F = 7.46
std. dev.	2.2	1.9	3.6	—	P = 0.0007
number	69	94	66	—	
Total pouches/paired branchiae					
mean	<u>9.6</u>	<u>8.4</u>	14.5	—	F = 16.97
std. dev.	2.7	2.7	11.5	—	P = 0.0001
number	69	92	66	—	

male of *S. gynobranchiata* from Copano Bay, Texas and one female of *S. shrubsolii* from Sully Island, Wales, larvae were produced after 12 days but were misshapen and did not survive. In two experimental crosses between males of *S. gynobranchiata* from Trinidad and planktotrophic females of *S. benedicti* from North Carolina, no larvae were produced. These results suggest that reproductive isolation is incipient between *S. gynobranchiata* and *S. benedicti* and between *S. gynobranchiata* and *S. shrubsolii*. Reproductive compatibility between populations is generally considered to be a pleisiomorphic characteristic, whereas loss of reproductive potential between closely related taxa can be considered an apomorphic characteristic. Considering the degree of morphological differentiation (Tables 1, 2) in addition to the differences in geographic range and reproductive isolation, it seems certain that *S. gynobranchiata* represents a new and distinct species.

At present, there appear to be at least four species of *Streblospio* that can be distinguished based upon morphological characteristics (Table 1). *Streblospio gynobranchiata* differs from *S. benedicti* in its more southern distribution, the presence of branchiate brood structures on females, the presence of posterior dorsal ciliated appendages in females, gamete distribution in females, and mature sperm dimensions. *Streblospio gynobranchiata* differs from *S. shrubsolii* in the distribution of hooded hooks (beginning on setiger 7 in the former species and setiger 8 in the latter), the incomplete dorsal collar in the latter species, and the absence of a prostomial nuchal tentacle in the latter species. *Streblospio gynobranchiata* differs from *S. benedicti japonica* in the distribution of ventral sabre setae (beginning on setiger 3 in the latter species) and in the number of paired small teeth on the hooded hooks [see Ohwada & Nishino (1991) for a discussion of variability in

this character]. In addition to the differences in standard morphological characteristics between *S. gynobranchiata* and the other described species in the genus, there are also differences in gamete morphology, gamete distribution (Table 2), modes of larval development, and reproductive compatibility.

*Phylogenetic relationships.*—The four species of *Streblospio* were analyzed for phylogenetic relationships using the cladistic programs, MacClade 3.01 (Maddison & Maddison 1992) and PAUP 3.1.1 (Swofford 1993). A character matrix consisting of 16 morphological and reproductive characteristics was constructed from literature reports and personal observations (Appendix 1). All characters were unweighted and unordered. The three most parsimonious trees found via an exhaustive search (Fig. 14A, B, C) all consist of 30 steps (consistency index = 0.933, retention index = 0.714) and were rooted using *Paraprionospio pinnata* and *Spiophanes kroyeri* as the designated outgroups. The strict consensus tree (Fig. 14D) groups *S. gynobranchiata* and *S. benedicti* as a clade with *S. benedicti japonica* and *S. shrubsolii* joining as a polytomy. More information is needed concerning the characteristics of these latter two species in order to resolve this node. A bootstrap analysis of 100 replicates in PAUP using tree-bisection-reconnection branch swapping, MULPARS activated, zero-length branches collapsed, and multi-state characters interpreted as polymorphism, resulted in the values listed on the branches in Fig. 14D.

Sigvaldadóttir et al. (1997) presented a cladistic analysis of the genera within the Spionidae based upon 25 morphological characters. Analysis of generic characteristics, including variation between species within a genus, resulted in a large number of most parsimonious trees (13305) and contributed little to our understanding of spionid relations. A second analysis using only type species as generic representatives produced more informative results with

four equally parsimonious trees. In the consensus tree derived from these four trees, *Streblospio benedicti* is grouped as the most plesiomorphic member of a clade including *Aurospio dibranchiata*, *Orthoprionospio cirriformia*, *Paraprionospio pinnata*, *Prionospio banyulensis*, *Prionospio steensrtupi*, and *Laubieriellus grasslei*. Sigvaldadóttir et al. (1997) point out that many characteristics of spionid genera are missing or incorrectly reported in the literature and that resolution of spionid phylogeny will likely require re-examination of species and development of new characters. Incomplete literature reports and polymorphic characters within species hampered resolution in the present study also. Four characters are coded as missing in the *Streblospio* data matrix for *S. benedicti japonica* since these four characters were not included in the description of the species by Imajima (1990). Knowledge of these characters would likely help to resolve the polytomy in the *Streblospio* consensus tree.

The study of variation within the genus *Streblospio* emphasizes the value of considering reproductive characters along with standard morphological traits when distinguishing traits within a polychaete genus. Eckelbarger and Grassle (1984) demonstrated a similar situation in which sibling species of *Capitella* are distinguished primarily by reproductive features. Characters such as strap-like branchiae in the genital region of females, the position and number of gametogenic setigers, and mature sperm dimensions distinguish *S. gynobranchiata* from other species of *Streblospio* (Table 1). In mature specimens, reproductive characters like brood structures are more readily observed than setal or ciliation patterns. Unfortunately, immature specimens of different species of *Streblospio* appear similar in overt morphology and care must be taken with identification in regions where more than one species is likely to occur (e.g., southern USA, Europe). We expect that additional sibling species of *Streblos-*

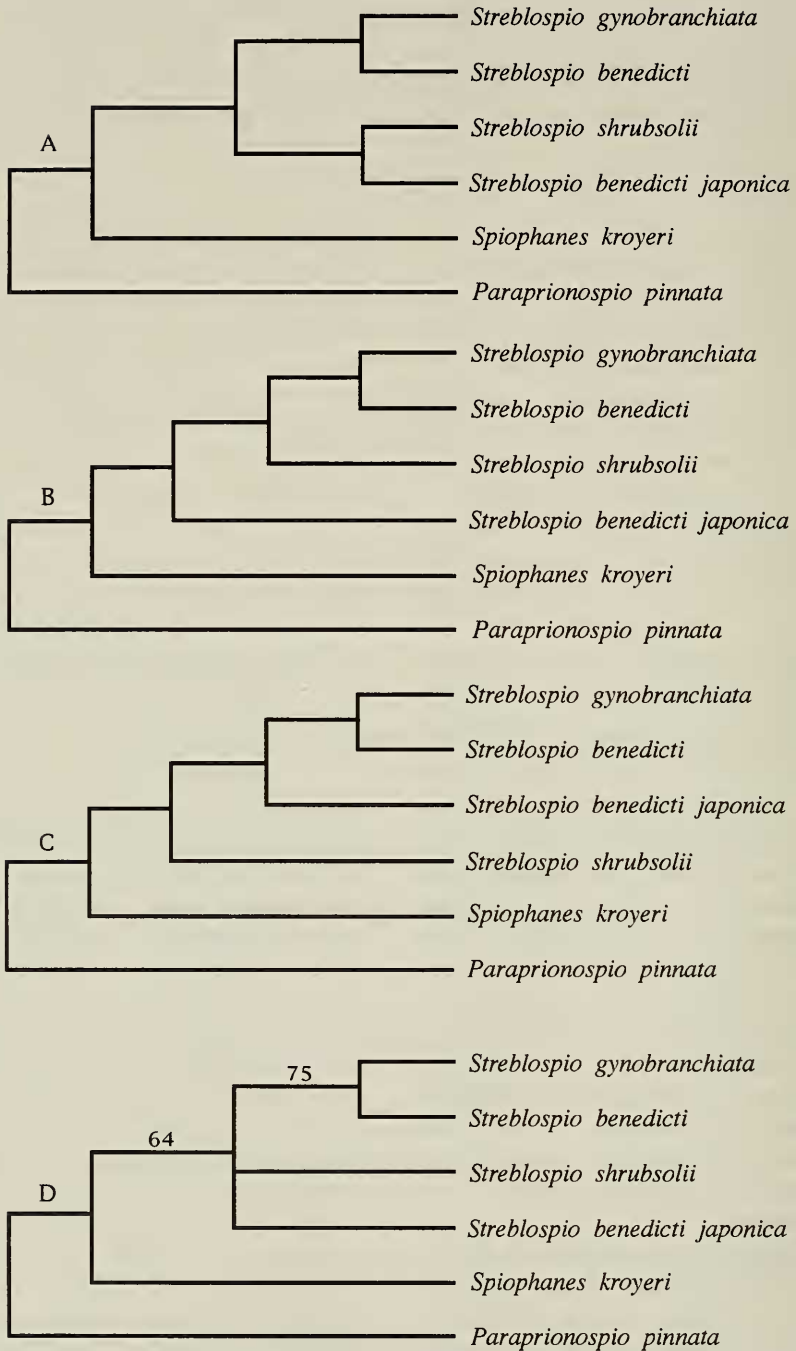


Fig. 14. A, B, C, three most parsimonious trees for the four species in the genus *Streblospio*. Each tree is 30 steps; D, strict consensus tree with bootstrap values listed on branches.



Table 3.—Character code data matrix.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>S. gynobranchiata</i>	1	1	0	1	0	1	1	2	1	1	2	1	0	0	1	1
<i>S. benedicti</i>	1	1	0	1	0	1	1	2	1	0	2	1	0	0/1	1	1
<i>S. shrubsolii</i>	0	1	1	2	0	0	1	1	1	2	?	0	0	2	1	1
<i>S. benedicti japonica</i>	0	1	0	1	0	?	1	2	1	?	0	2	1	?	1	1
<i>Paraprionospio pinnata</i>	1	0	1	3	1	2	0	0	0	2	3	0	2	0	1	1
<i>Spiophanes kroyeri</i>	0	1	0	4	2	1	0	0	2	2	1	?	2	?	0	0

*pio* will emerge as reproductive, genetic, and morphological characters of populations around the world are examined in greater detail.

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Appendix 1.—Character codes for phylogenetic analysis of *Streblospio* species (and Table 3).

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1. *Total number of segments*
    - 0: <50
    - 1: >70
  2. *Membrane on palps*
    - 0: present
    - 1: absent
  3. *Nuchal antenna*
    - 0: present
    - 1: absent
  4. *First hooded hook*
    - 0: 6th setiger
    - 1: 7th setiger
    - 2: 8th setiger
    - 3: 9th setiger
    - 4: 15th setiger
  5. *Pairs of Branchiae*
    - 0: 1 pair
    - 1: 3 pair
    - 2: none
  6. *Hooks per posterior ramus*
    - 0: 5
    - 1: 8–12
    - 2: >12
  7. *Notopodial hooks*
    - 0: present
    - 1: absent
  8. *Dorsal collar at setiger 2*
    - 0: absent
    - 1: 2 lobes
    - 2: 1 lobe
  9. *Anterior postsetal lamella*
    - 0: auricular
    - 1: semicircular
    - 2: pointed
  10. *Brood structures*
    - 0: pouches
    - 1: branchiae
    - 2: none
  11. *First sabre seta*
    - 0: 3rd setiger
    - 1: 4th setiger
    - 2: 7th setiger
    - 3: 9th setiger
  12. *Small teeth on hooded hooks*
    - 0: 2 pair
    - 1: 3 or 4 pairs
    - 2: 5 pairs
  13. *Pygidium*
    - 0: simple
    - 1: ventral lappets
    - 2: lobes and cirri
  14. *Larval development*
    - 0: planktotrophic
    - 1: lecithotrophic
    - 2: direct
  15. *Body regions*
    - 0: distinct
    - 1: graded
  16. *Neurosetal spines*
    - 0: present
    - 1: absent
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